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SOCIAL LIFE AMONG THE INSECTS[1]

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LECTURE II. WASPS SOLITARY AND SOCIAL

IN the preceding lecture I gave a brief account of the rudimentary social life of certain beetles and called attention to the fact that in all or nearly all of them the male cooperates with the female parent in victualing or protecting the offspring. I endeavored to show that all these societies have their inception or *raison d'être* in the specialized feeding habits of the parents and that in all of them the food is of vegetable origin, abundant but not very nutritious in some of the cases (dung and rotten wood in the Scarabæidæ, Passalidæ and Phrenapates), in others highly nutritious, but obtainable only in small quantities at a time (living plant-tissues and honey-dew in the case of the Tachigalia beetles, ambrosia of the Ipidæ and Platypodidæ). The adequate exploitation of such food-supplies is necessarily time-consuming and has evidently led to a lengthening of the adult lives of the beetles. This in turn has naturally brought about an overlapping of the juvenile by the parent generation, thus enabling the parents to acquire contact and acquaintance with their young and an interest in providing them with the same kind of food as that on which they themselves habitually feed. In the insects which I shall consider in this lecture, we find a series of societies originating in a very different type of feeding and leading to much more complicated and more definitely integrated associations.

Although the wasps have attracted fewer investigators than the ants and bees, they are of even greater interest to the student who is tracing the evolution of specialized instincts and social habits. The wasp group is one of enormous size and is really made up of two great complexes, the Sphecoids and the Vespoids, together comprising more than a dozen families and some 10,000 species. Of these only about 800 are clearly social. We have more or less fragmentary behavioristic studies of scarcely 5 per cent. of all the species. Yet they cover a sufficient number of forms to enable us to establish the following generalizations:

(1). The structure and behavior of the Sphecoids and Vespoids show that they must have arisen from what have been called Parasitic Hymenoptera, and the structure of the ants and bees shows that they in turn must have arisen from primitive Sphecoids or Vespoids.

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[1] Lowell Lectures.

(2). The social wasps comprise several groups which have evolved independently from primitive, solitary Vespoids, but there are also a few Sphecoids that exhibit subsocial propensities.

(3). Both the Sphecoids and the Vespoids are primarily predaceous and feed on freshly captured insects, but the adults are fond of visiting flowers and feeding on nectar. Some social wasps store honey in their nests, but it is probably not an exclusive or essential constituent of the larval food. One small and aberrant group of solitary Vespoids, the Masarinæ, however, provision their cells with a paste of honey and pollen, like the solitary bees. The insect prey on which at least the young of nearly all the wasps subsist, being extremely rich in fats and proteids, is an ideal food, but has to be provided in larger quantity than such concentrated vegetable substances as pollen and nectar. It is also scarcer and more difficult to obtain. Hence the definite tendency in adult wasps towards a honey regimen at least for the purpose of eking out the primitive animal diet.

(4). We are able to observe in the social wasps more clearly than in other social insects the peculiar phenomenon which I have called "trophallaxis," *i. e.*, the mutual exchange of food between adults and their larval young.

(5). The study of the wasps and of their ancestors among the Parasitic Hymenoptera furnishes us with a key to the understanding of parthenogenesis and the peculiar dominance of the female sex (gynarchy) which is retained throughout the whole group of stinging Hymenoptera (wasps, bees and ants).

(6). In the social wasps we witness the first gradual development of a worker caste and also of polygyny and swarming.

(7). We observe in wasps a high degree of modifiability of behavior and an extraordinary development of memory, endowments which have led McDougall to claim for them "a degree of intelligence which (with the doubtful exception of the higher mammals) approaches most nearly to the human," and Bergson to point to their activities as one of the most telling arguments in favor of his intuitional theory of instinct. Although I believe that these and many other authors have been guilty of some exaggeration the wasp's psychic powers compared with those of most other insects or even of many of the lower Vertebrates seem to me, nevertheless, to be sufficiently remarkable.

We shall have to examine each of these generalizations more closely. Some of them may be considered forthwith, others more advantageously after the description and illustration of a selected series of species.

Recent studies of the parasitic, or as I prefer to call them with O. M. Reuter, the "parasitoid" Hymenoptera, have revealed certain peculiar traits which recur in a modified form in the behavior of their Sphecoid and Vespoid descendants. But what are these parasitoids? You are all familiar with the fact that a large number of insects regularly lay their eggs on or in plants and that the hatching larvæ devour the plant tissues and eventually pupate and emerge as insects which repeat the same cycle of behavior. There is, however, another immense, but less conspicuous, assemblage of insects that lay their eggs on or in the living eggs, larvæ, pupæ and adults of other insects, and the eggs thus deposited develop into larvæ which gradually devour the softer tissues in which they happen to find themselves. Species that behave in this manner are not true parasites, but extremely economical predators, because they eventually kill their victims, but before doing so spare them as much as possible in order that they may continue to feed and grow and thus yield fresh nutriment just as it is needed. For this reason and also because, as a rule, only the larval insect behaves in the manner described, it is best called a "*parasitoid.*" The adult into which it develops is, in fact, a very highly organized, active, free-living creature, totally devoid of any of the stigmata of "degeneration" so common among parasites, and with such exquisitely perfected sensory, nervous and muscular organs that it can detect its prey in the most intricate environment and under the subtlest disguises.

The parasitoids exhibit another peculiarity which was destined to acquire great importance in their descendants, the wasps, bees and ants, namely, parthenogenesis, or the ability of the female to lay unfertilized eggs capable of complete development. As a rule, if not always, these parthenogenetic eggs develop into males, whereas fertilized eggs laid by the same female develop into individuals of her own sex. Thus the female has become to some extent independent of the male in the matter of reproduction. It will be seen that if the parthenogenetic egg were able to develop into a female, as it frequently does in certain insects like the plant-lice, the male might become entirely superfluous. There are a few insects in which this has occurred or in which the male appears only at infrequent intervals in a long series of generations. But matters have not come to such a pass in the parasitoids or in the wasps, bees and ants, though these insects have perfected another method of reducing the male to a mere episode in the life of the female. Individuals of this sex are provided with a small muscular sac, the spermatheca, which is filled with sperm during the single act of mating, and this sac is provided with glands, the secretion of which may keep the sperm alive for months or even years. According to a generally accepted theory, the female can voluntarily contract the wall of her spermatheca and thus permit sperm to leave it and fertilize the eggs as they are passing its orifice on their way to being laid, or she can keep the orifice closed and thus lay unfertilized eggs. The mother can thus control the sex of her offspring or if she has failed to mate, or has exhausted all the sperm in her spermatheca, may nevertheless be able to lay male-producing eggs. There seems also to be something compensatory, or regulatory, in this ability of the female parasitoid to produce males parthenogenetically, for if she be unable to meet with a male—and this predicament is very apt to arise among such small and widely dispersed animals as insects—she can produce the missing sex and thus increase the chances of mating for the next generation of females.

Certain facts indicate that the sex of the egg may not be determined in the manner here described, but their consideration must be postponed till they can be taken up in connection with the honey-bee. We are justified, notwithstanding, in regarding the female parasitoid, wasp, bee or ant, after she has appropriated and stored in her spermatheca all the essential elements of the male, as a potential hermaphrodite. The body, or soma, of the male, after mating, thus really becomes superfluous and soon perishes. In the solitary wasps the male is a nonentity, although in a few species he may hang around and try to guard the nest. But in the bees, ants and social wasps he has not even the status of a loafing policeman, and all the activities of the community are carried on by the females, and mostly by widows, debutantes and spinsters. The facts certainly compel even those who, like myself, are neither feminists nor vegetarians, to confess that the whole trend of evolution in the most interesting of social insects is towards an ever increasing matriarchy, or gynarchy and vegetarianism.

Now if we carefully observe a parasitoid while she is ovipositing in her prey, we obtain a clue to the meaning of the peculiar behavior of the solitary wasps which has led Fabre to certain erroneous conclusions and philosophers like Bergson to his peculiar interpretation of instinct. The parasitoid is furnished at the posterior end of her body with a well-developed ovipositor, a slender, pointed instrument for piercing the tough integument of her victim. But this instrument also has another function, namely, that of making punctures through which droplets of the victim's blood may exude and be devoured by the parasitoid. She may often be seen thrusting her ovipositor into her prey without ovipositing and merely for the sake of obtaining food, or she may feed at a puncture she has made while ovipositing. Obviously feeding and oviposition are here congenitally, or hereditarily conditioned reflexes, to use Pawlow's expression. In other words, the internal hunger and reproductive stimuli, or appetites, are so intimately associated with one another that mere contact with the prey releases either the feeding or the ovipositing reactions, or both. And, of course, both of these reactions are purely selfish, the one being concerned with getting food, the other with getting relief from the discomfort of egg-pressure in the ovaries, and both may initiate elaborate trains or patterns of behavior (instincts). This is true not only of the parasitoids but also of insects in general.

Turning now to the solitary wasps we find that, like the parasitoids, they prey on other insects and that each species of wasp usually has a predilection for a particular species (Figs. 18 and 19), genus or family of insects, or even for a particular sex, as in the case of one of our common wasps, *Aphilanthops frigidus,* which preys only on queen ants. The chief difference

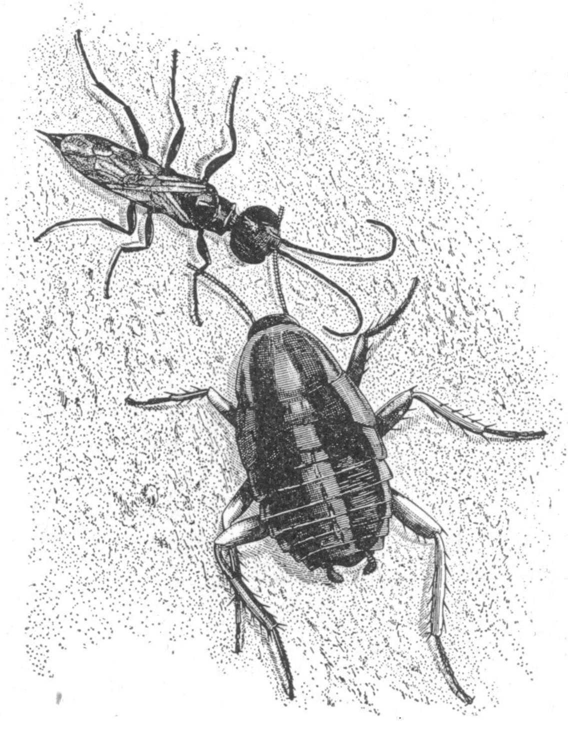

FIG. 18

Dolichurus stantoni of the Philippines dragging a young cockroach (*Blatella bisignata*) to her burrow. x 6. (After F. X. Williams).

between the parasitoid and the solitary wasp lies in the fact that the latter lays her egg on or near her victim after stinging it till it is motionless. The sting is merely the ovipositor which is now used only for defence or for reducing the prey to impotence, while the mouth-parts and especially the mandibles are used for obtaining food. Many solitary wasps, after stinging their prey,

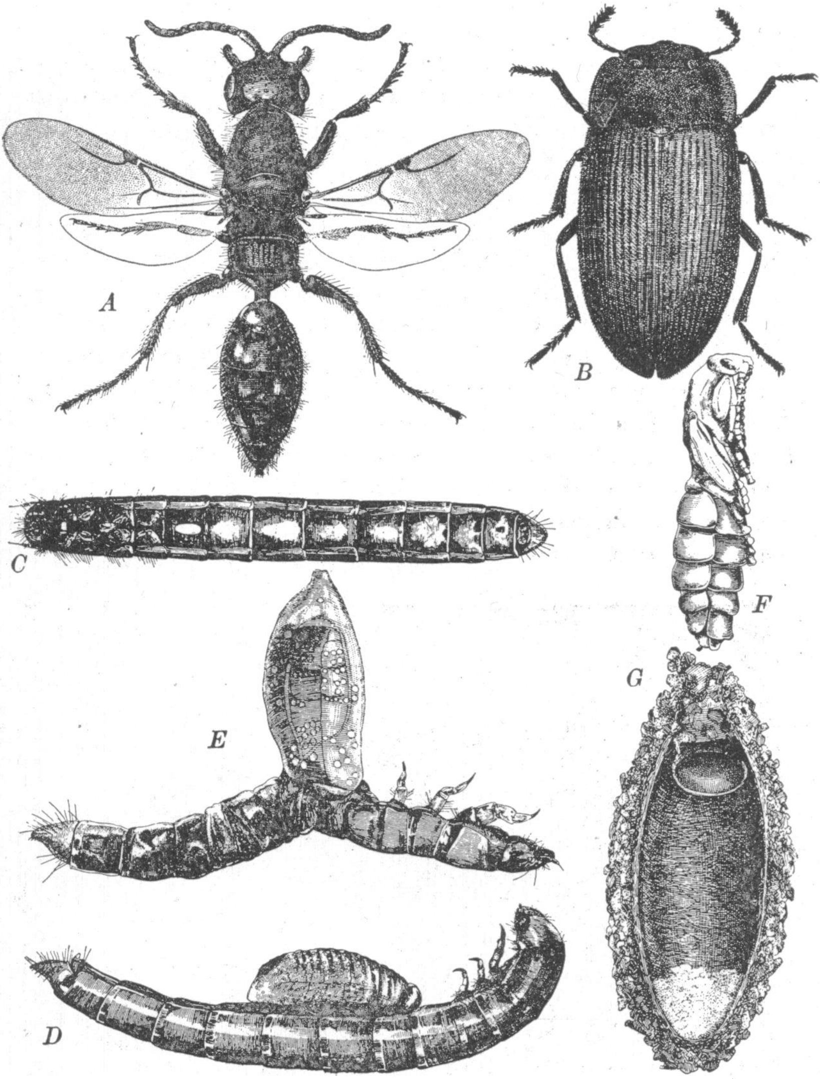

FIG. 19

A. Female of a Bethylid wasp *Epyris extraneus,* of the Philippines; B. Tenebrionid beetle, *Gonocephalum seriatum;* C. Larva of the same with egg of *E. extraneus* on middle of ventral surface; D. Young *E. extraneus* larva feeding on the larva of *G. seriatum;* E. Later stage of same; F. Pupa of *E. extraneus;* G. Cocoon of same. (After F. X. Williams).

devour it in part or entirely, or chew, *i. e.*, malaxate, its neck and lap up the exuding juices. This behavior is essentially like that of the parasitoid, and in its more frequent, feebler manifestations may be regarded as a vestigial feeding. The adult wasp is no longer as carnivorous as its ancestors, because she has come to rely to some extent on the energizing nectar of flowers, but this substance contains no proteids and is therefore an improper food for her growing larval young. Roubaud and Rabaud have recently shown that the stinging of the prey follows reflexly as soon as it has been seized and comes in contact with the wasp's sternum, and that the accidental position of the prey when it thus releases the reflex determines the point where it will be stung. Moreover, the stinging is repeated till the victim ceases to struggle and becomes motionless. Hence the stinging does not occur in the schematic manner nor necessarily in the nerve ganglia, as described by Fabre. It has also been shown that the venom introduced into the tissues of the prey by the sting produces paralysis or even death and also acts as an antiseptic in preserving the prey from decomposition for weeks or even months while the larva that hatches from the wasp's egg is feeding on the tissue, but these properties of the venom are accidental and unforeseen. Hence Fabre's and Bergson's contention that the solitary wasp is a clairvoyant surgeon, with an intuitive knowledge of the internal anatomy of the particular insect on which it preys, may be dismissed as a myth.

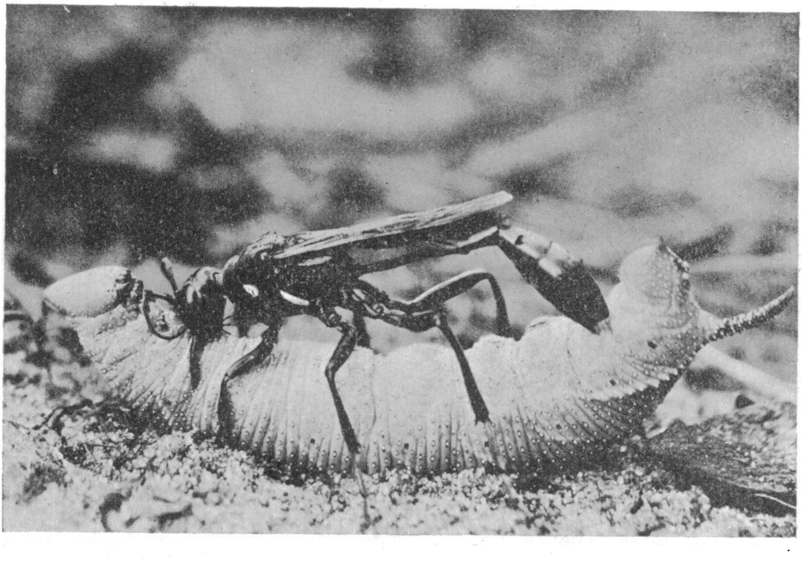

FIG. 20

Sphex procerus carrying caterpillar of sphinx moth to her burrow. (Photograph by Prof. Carl Hartman).

The explanations here given of the malaxation and stinging of the prey are purely physiological, but it is not at all certain that such explanations are applicable to the entire behavior cycle of the solitary wasp. Before enquiring into this matter, it will be advisable to sketch very briefly the behavior of a typical Sphex as a paradigm of the whole group of Sphecoids and solitary Vespoids. The female Sphex, after mating, digs in sandy soil a slanting or perpendicular tunnel and widens its end to form an elliptical chamber. She may thereupon close the entrance, rise into the air and fly in undulating spirals over the burrow, thus making what is called a "flight of orientation," or "locality study," because it enables her to fix in her sensorium the precise position of the burrow in relation to the surrounding objects, so that she may find the spot again. Then she flies off in search of her prey, which is a particular species of hairless caterpillar (Fig. 20). When it is found, she stings it into insensibility, malaxates its neck, while imbibing the exuding juices, and drags it or flies with it to the entrance of her burrow. Here she drops her victim and, after entering and inspecting the burrow, returns and takes it down into the chamber, glues her egg to its surface and closes the burrow by filling it with sand or detritus collected from the surrounding soil (Figs. 21 and 22). As soon as the next egg matures in her ovaries she proceeds to repeat the same behavior cycle at some other spot. In the meantime the provisioned egg hatches, and the

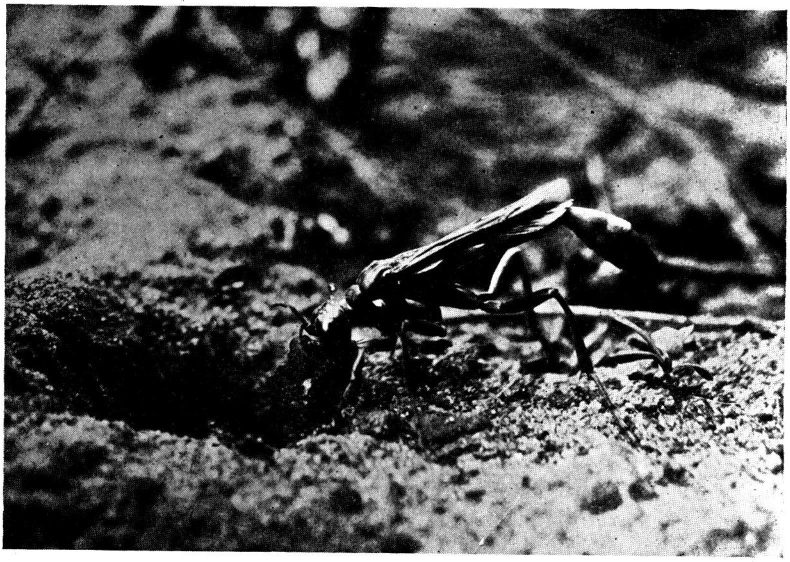

FIG. 21

Sphex procerus carrying chips of wood to throw into the burrow at the left of the figure. (Photograph by Prof. Carl Hartman).

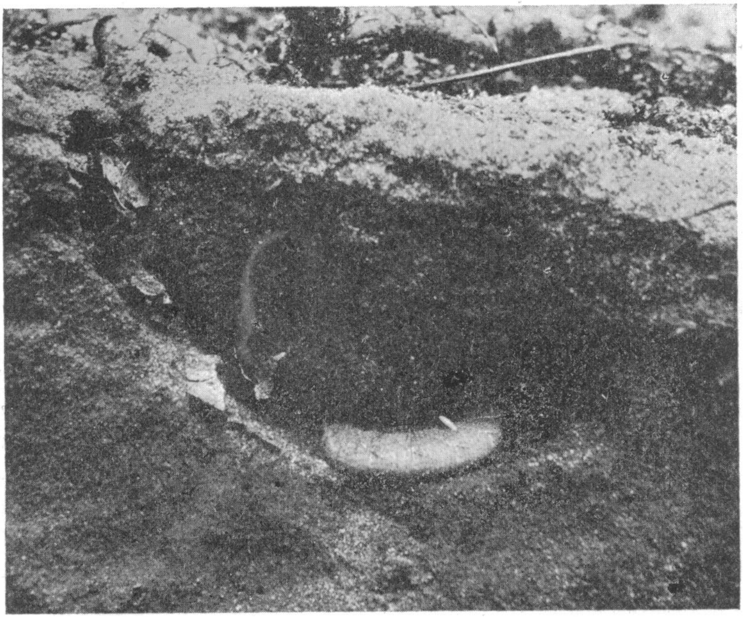

FIG. 22
Burrow of *Sphex procerus* in section, showing filling of débris in the tunnel and the paralyzed sphinx moth caterpillar in the cell, with the egg glued to its side. (Photograph by Prof. Carl Hartman).

larva, after devouring the helpless caterpillar, spins a cocoon, pupates *in situ* and eventually emerges as a perfect Sphex.

Some of our species of Sphex actually tamp down the filling of their burrows with a small, carefully selected pebble, held in the mandibles and used as a hammer or pestle (Fig. 23). This

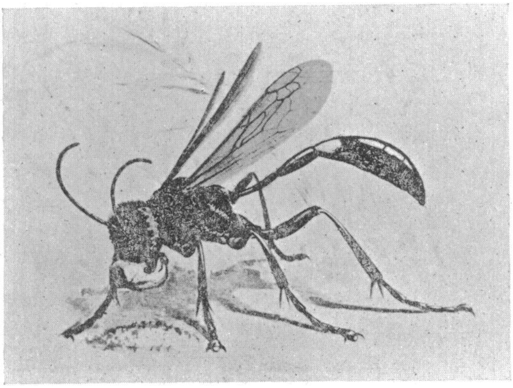

FIG. 23
Sphex urnarius using a selected pebble to pound down earth over burrow. (After G. W. and E. G. Peckham).

astonishing behavior, which has been carefully observed by no less than nine investigators (Williston, Pergande, Geo. W. and E. G. Peckham, Hartman, Hungerford and Williams, and Phil. and Nellie Rau) can hardly be reduced to simple physiological reflexes. The same would seem to be true of the orientation flight and return to the burrow and the fact that some species of Sphex provide the egg with a single large caterpillar, others with several small caterpillars, but in all cases with just enough food to enable the larva to grow to the full stature of a normal individual of its species. The question also arises as to the proper interpretation of the peculiar predilection of the wasp for a particular species of prey. This seems to be the more inexplicable, because experiment has shown that the larva can be successfully reared when some very different insect is substituted for the species which it habitually devours. As I am emphasizing the rôle of nutrition in these lectures, I shall digress somewhat on this question of food specialization and in order to bring the matter before you as vividly as possible recast the behavior of Sphex in the form of a tragic drama in three acts, with the following brief synopsis:

Act I. A sandy country with sparse vegetation inhabited by caterpillars and other insects. Time, a hot, sunny day in early August. Scene 1. Miss Sphex arrayed in all the charm of maidenhood being courted by Mr. Sphex. Wedding among the flowers. Scene 2. Mrs. Sphex deserted by her scatter-brained spouse settles down and excavates a kind of cyclone-cellar. She closes its door and leaves the stage.

Act II. Scene 1. Same as in Act I. Mrs. Sphex, hunting in the vegetation, finds a caterpillar, struggles with it, stings it and gnaws its neck till it lies motionless. Scene 2. She drags it into the cellar and placing her offspring on it behind the scenes, returns and at once leaves the stage after locking the door, amid a storm of applause.

Act III. Scene 1. Interior of Mrs. Sphex's cellar. Baby Sphex slowly devouring caterpillar till only its skin remains. Scene 2. Baby Sphex, now a large, buxom lass, weaves an elaborate nightgown for herself and goes to bed as the curtain falls.

As a work of art this drama is defective, because the climax, the stinging of the caterpillar, falls in the early part of the second act, and because the heroine leaves the stage soon afterwards for good, as if she had been suddenly taken ill and had to substitute her drowsy offspring to perform the whole third act. Still this is the sequence in which the drama is related by all the observers, and I have presented my account in the same manner, because it has undeniable advantages. But see what happens when we rearrange the drama by making the third or last act the first, and the first and second the second and third, respectively. There is then only one heroine who holds the center of the stage throughout the performance. We witness her gradual growth and development from infancy during the first act, her wedding, desertion and cellar-excavating exploits during the second, and the thrilling chase, stinging and entombment of the hereditary victim in the third act.

I have just committed the unpardonable sin of humanizing the wasp, but being desirous of making my point perfectly clear, I am going to do something still more scandalous and ask you for a moment to vespize the human being. Suppose that the human mother were in the habit of carefully tying her new-born baby to the arm-pit of a paralyzed elephant which she had locked in a huge cellar. The baby—we must, of course, suppose that it is a girl baby—is armless, legless and blind, but has been born with powerful jaws and teeth and an insatiable appetite. Under the circumstances she would have to eat the elephant or die. Supposing now that she fed on the elephant day after day between naps till only its tough hide and hard skeleton were left, and that she then took an unusually long nap and awoke as a magnificent, winged, strong-limbed amazon, with a marvellously keen sense of smell and superb eyes, clad in burnished armor and with a poisoned lance in her hand. With such attractions and equipment we could hardly expect her to stay long in a cellar. She would at once break through the soil into the daylight. Now suppose she happened to emerge, with a great and natural appetite, in a zoological garden, should we be astonished to see her make straight for the elephant house? Why, she would recognize the faintest odor of elephant borne to her on the breeze. She would herself be, in a sense, merely a metabolized elephant. Of course, we should be startled to see her leap on the elephant's back, plunge her lance into its arm-pit, drag it several miles over the ground, hide it in a cellar and tie her offspring to its hide.

The point I wish to make is this: We have all along in our accounts treated the life-history of the insect as that of two individuals in such a manner as to obscure or obliterate the experience of the individual. We begin with the full-fledged insect descending from the blue, and then describe her behavior as if it were a pure inheritance or improvisation. But when we describe her activities as those of a single individual from the beginning of her development to death, we find that the adult female, before she begins to make and provision her nest, has probably learned something from her long and intimate larval contact with the environment. For months she has inhabited a chamber like the one she will excavate or build for her own progeny, for days she has been devouring a particular species of caterpillar and she has even dug a sufficient distance through the soil to be familiar with its properties. She possesses, therefore, a certain amount of acquaintance with soil and with caterpillars. That this should persist as memory is not only possible but extremely probable when we consider that the central nervous system of the larva passes without profound change into that of the adult wasp and that the latter shows unmistakable evidence of possessing a remarkable memory when she makes such locality studies as have been described and returns to her nest or prey after an absence of several hours or even days. We are also enabled to understand why the wasp confines her attention to a particular species or even to one sex of a species while searching for her prey, and why the malaxation or mutilation of the prey may be regarded as a reminiscent act of feeding. In brief, all those activities of the adult wasp which are partly or wholly interpretable as a repetition of larval behavior, may be attributed to memory—not in the sense of recollection, with its feeling of "pastness," but of mere sensory and motor memory, the *memoria sensitiva* of scholastic writers, or the "associative memory" of comparative psychologists.

But there still remain unexplained the more striking activities, those performed for the first time in the wasp's life-history, namely the cocoon-spinning of the larva, the making, closing and opening of the nest, oviposition, etc. No doubt these acts are all initiated by stimuli, partly internal and partly external, such as hunger, the tension of accumulated silk in the spinning glands, of eggs in the ovaries, hormones in the blood, and olfactory and tactile impressions from contact with the caterpillar and the soil, but the reeling off of the train of these purposive responses must depend on inherited dispositions in some way correlated with the structure of the nervous and muscular apparatus. And we must suppose that these dispositions somehow represent the experience of untold former generations of wasps. We are, however, unable to form any adequate conception of the extent of the racial experience of the solitary wasps as a group and therefore of the amount of condensation or syncopation with which it is epitomized in the behavior of the individual wasp, and this disability on our part is largely responsible not only for the old supernatural conceptions of instinct but also for theories like those of Bergson, the Neodarwinians and the mutationists.

We may now turn to the evolution of social behavior, which, in diverging lines of descent, has been gradually evolved and perfected from such a method as that employed by most of the

Sphecoids and non-social Vespoids. This method, which consists in rapidly accumulating an amount of prey sufficient to enable the young to develop to maturity and of then closing the cell before the egg has hatched, we may designate, with Roubaud, as "mass provisioning." We have seen that in some cases the mother wasp stores a single large insect, in others a number of smaller ones, before closing the cell. If in the latter case the accumulation of the prey is delayed on account of scarcity or inclement weather, the egg, which has been glued to the first small insect captured, hatches before the mother wasp has succeeded in collecting a sufficient supply for the growth of the larva. She is therefore reduced to feeding her offspring from day to day, *i. e.*, to what Roubaud calls "progressive provisioning," a method which is seen in certain species of Sphex and Lyroda (*S. politus* and *L. subita,* according to Adlerz) and probably also in *Aphilanthops frigidus,* according to my observations. But the best examples may be observed among the digger-wasps of the family Bembicidæ, on which we possess a number of valuable studies by Wesenberg-Lund, Bouvier, Marchal, the Peckhams, Hartman, Riley, Melander, Ferton, Parker, Adlerz, the Raus, etc. While our large cicada-killer (*Sphecius speciosus*) provisions its burrows with a single cicada, lays an egg on it and closes the cell, thus practicing typical mass provisioning, some other Stizinæ and many species of Bembix and allied genera proceed in a different manner. These insects live in open, sandy places, often in rather populous and compact congregations, though each female makes and provisions her own burrow. The prey of each species of Bembix consists of the common two-winged flies of her environment, without regard to the species. They are stung to death but not mutilated. After the burrow is excavated the wasp kills a small fly and after dislocating one of its wings, places it on its back on the floor of her cell and attaches her egg to its sternum. The dislocation of the wing is supposed by Ferton to be a device for preventing the fly from being turned over by the very delicate young larva and thus insuring it against injurious contact with the rough, sandy floor of the cell. The mother collects flies and brings them into the burrow from day to day, actually increasing the size or number of the victims as they are needed by the growing and increasingly voracious larva. At least one European species of Bembix (*B. mediterraneus*), according to Ferton, lays her eggs on the floor of the cell before bringing in any flies. Instead of flies, the species of Bicyrtes and Stizus provision their young progressively with bugs or leaf-hoppers, and one of our species (*Microbembex monodonta*), according to Hartman, Parker and the Raus, feeds its young on all sorts of small, dead and dried insects (grasshoppers, beetles, flies, mayflies, ants, etc.) picked up from the soil.

Among several of the solitary Vespoids we find very similar conditions and these are of more immediate interest to us because this group of insects has evidently given rise to the true social wasps. The numerous species of Eumenes and Odynerus (Fig. 24), as well as the allied genera, either excavate their burrows in the ground, or take possession of the tubular cavities of twigs or the interstices of walls, or construct exquisite mud cells above ground on the surfaces of rocks, trees or walls. After the cell is completed the egg is hung by a filament from its ceiling. Numerous small, smooth, paralyzed caterpillars are then brought in and the cell is closed. This is, of course, typical mass provisioning. But Roubaud has observed some very significant modifications of the process in certain Congolese species. Of one Odynerus (*O. tropicalis*) he gives the following account: "This little Odynerus does not

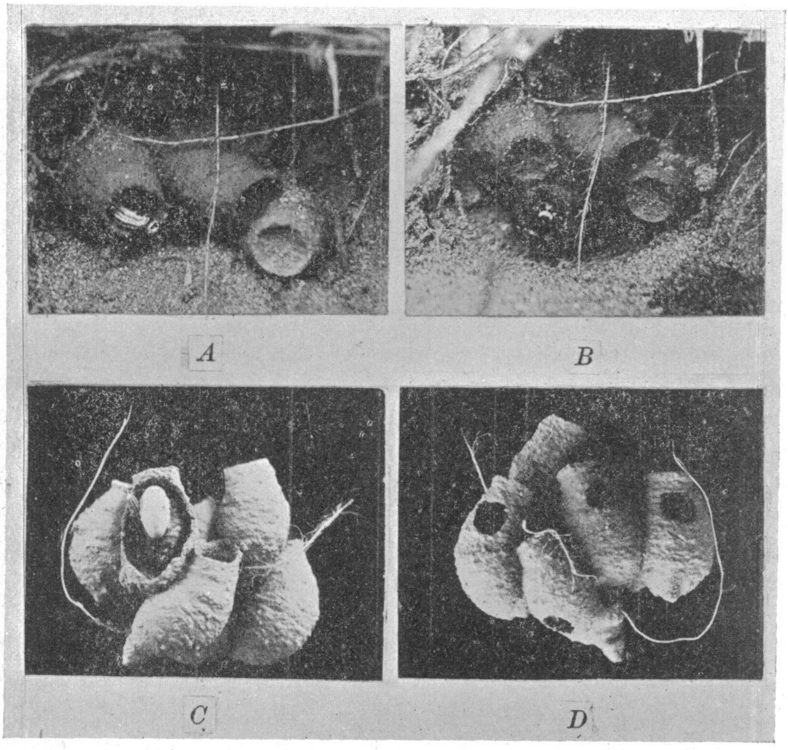

FIG. 24

Four stages in the mud nest of *Odynerus dorsalis*. *A*. Showing one cell open and being stored with small caterpillars; *B*. Nest on the following day, showing wasp resting in a new cell made on the previous afternoon. *C*. Nest with one cell opened to show the wasp larva feeding on caterpillars; *D*. Same nest, showing holes made by the escaping wasps. (After Carl Hartman).

provision its cells with prey amassed in advance, but nourishes its larvæ from day to day, with small, entire, paralyzed caterpillars, which are always given to the larva in very small numbers, till its growth is completed. The egg is never walled up in the cell with provisions hastily amassed. The wasp, to judge from what I have been able to observe of its educative procedure, after having laid her egg, watches it within the cell after the manner of the higher species of Synagris till it hatches. As a rule, prey is brought to the egg only at the moment of hatching or a little before, and usually a single small caterpillar, rarely two and never three, is found placed at the disposal of the just-hatched larva. *Pari passu* with the growth of the latter the prey is renewed, but always in small numbers. Sometimes the larva may be seen fasting in the cell while the mother wasp is away in search of prey. Finally, it is only after its feeding has been completed that the larva is immured in the cell. In no case did I observe in closed cells containing larvæ the slightest trace of provisions.'' Even more interesting are the species of Synagris referred to in this quotation. In several of them Roubaud found the following conditions, representing transitions from mass to progressive provisioning:

The female of *Synagris spiniventris* (cited as *callida* by Roubaud) and *callida* (cited as *sicheliana*) under normal conditions, *i. e.*, when food is abundant, lays an egg in her mud cell, fills it in the course of a few days with small paralyzed caterpillars, sometimes to the number of 60 (!) and then closes it, thus adopting the usual or ''banal'' method of mass provisioning. When, however, owing to seasonal or climatic conditions, caterpillars are scarce, the female, after ovipositing and guarding the egg for some time, collects a meager provision of small caterpillars for the hatching larva and while it is growing, continues to feed it in the same manner. After the larva has attained three fourths of its adult size, the wasp immures it in its cell with the last supply of provisions. As Bequaert remarks, ''in *S. spiniventris*, progressive provisioning is still optional, and one observes all the transitional stages between this behavior and the normal provisioning in mass. The mother wasp shows great skill in adapting her habits to the external conditions.'' According to Roubaud another species of Synagris (*S. cornuta*), proceeds a step further (Figs. 25 and 26). The female, after completing her earthen cell, lays an egg on its floor and when the larva hatches feeds it from day to day with pellets made of a paste of ground up caterpillars. This is precisely the method employed by the social wasps in feeding their larvæ!

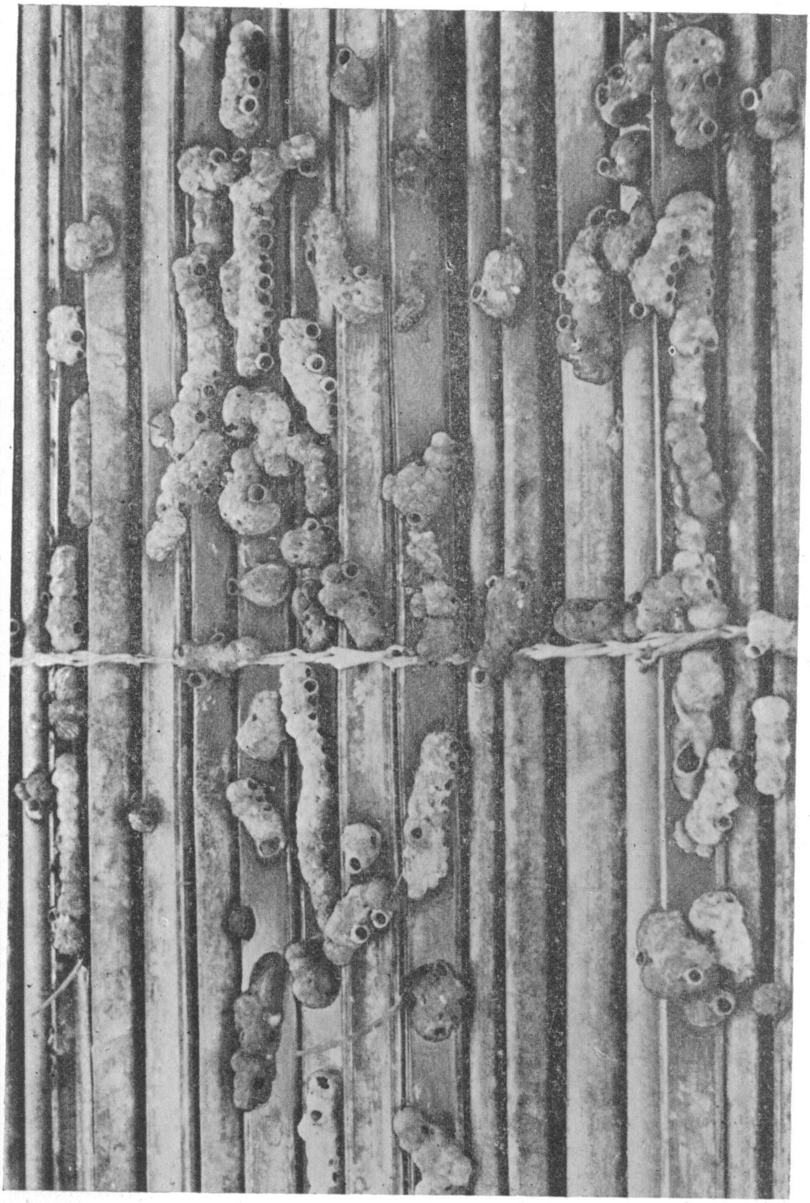

FIG. 25

Mud nests of *Synagris cornuta* on the thatching of a native hut in the Congo. "Some of these nests show very distinctly the short neck with its slightly widened opening curved to the side and downwards. Such a chimney is built at the entrance of the cells containing eggs or larvæ still nursed by a female." (After J. Bequaert from a photograph by H. O. Lang).

A step in the direction of the social wasps seems also to have been taken by a small group of solitary Vespoids, allied to the Eumeninæ, namely the Zethinæ. These insects, which have been studied recently in Brazil by Ducke, in British Guiana by Howes and in the Philippines by F. X. Williams, have abandoned the use of earth as nest material and employ instead small bits of leaves or moss (Fig. 27). With such vegetable material *Zethus* constructs a beautiful nest with one or several tubular cells, and therefore approaches the social wasps which make their nests of paper, a substance consisting of fine particles of wood agglutinated with an oral secretion. The egg is laid loosely in the bottom of the cell and, according to Williams' account of the Philippine *Zethus cyanopterus,* the larva is fed from day to day on small caterpillars, which have been in part eaten by the mother. She faithfully guards the larva and, while it is small and there is still ample room, sleeps in the cell. She closes the latter as soon as the larva is full grown and proceeds to build another.

Each of these cases of progressive provisioning may be regarded as a very primitive family, or society, reduced to its simplest terms, *i. e.,* to a mother and her single offspring. The seasonal or local conditions of the environment, in so far as they affect the abundance or scarcity of prey, have led on the one hand to mass provisioning and therefore to an exclusion of the mother from contact with her growing offspring, and on the other to an establishment

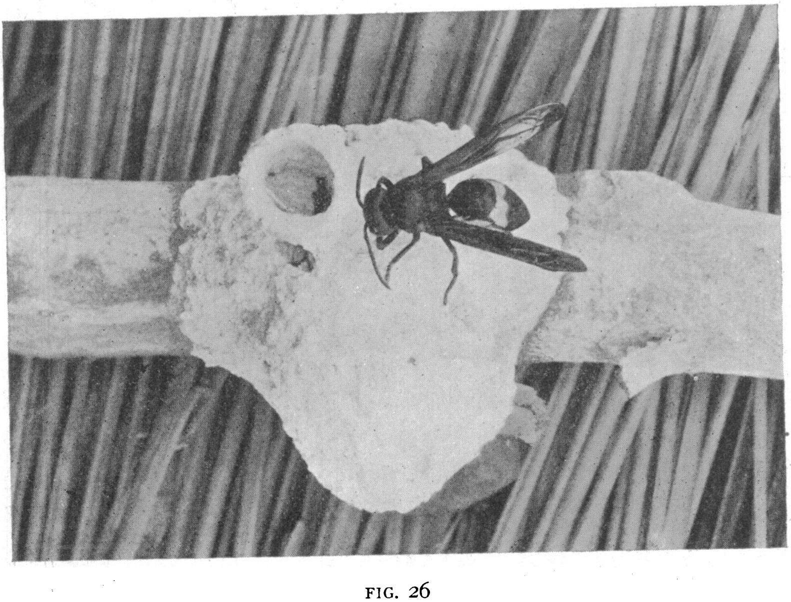

FIG. 26
Mud nest of *Synagris cornuta* var. *flavofasciata* with mother wasp. (After J. Bequaert from a photograph by H. O. Lang).

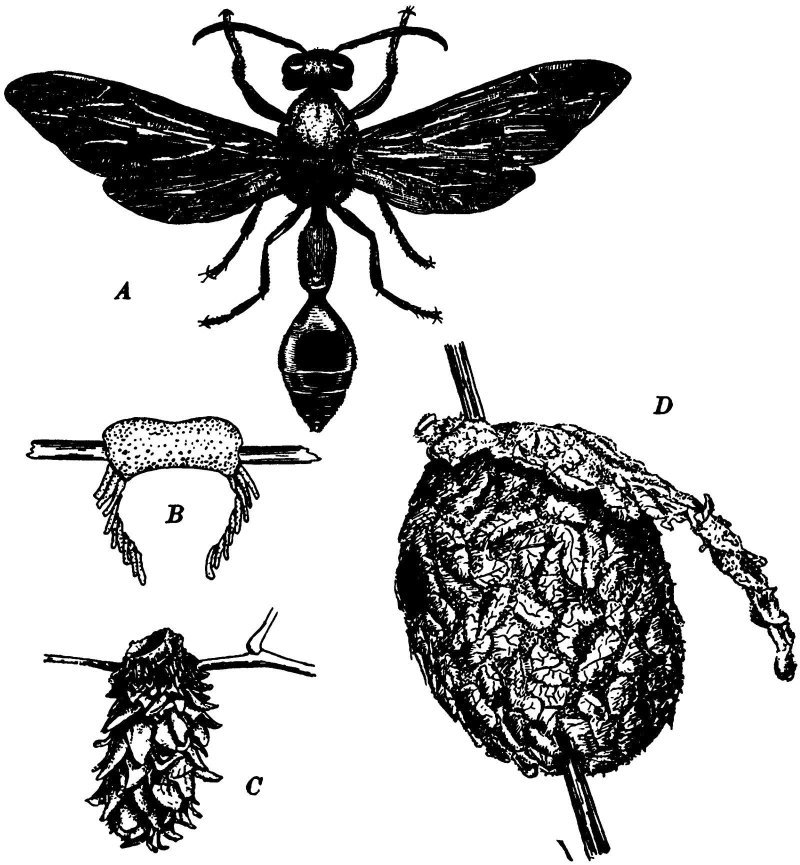

FIG. 27
Zethus cyanopterus of the Philippines and its nest. *A,* Adult wasp x 2; *B,* the beginning of a cell. It is attached to a twig by a mass of well-masticated leaf-bits and the wall of the cell is made of shingled leaf bits. (Somewhat enlarged); *C,* the first cell of the nest completed x ¾; *D,* a four-cell nest showing roof-like structure and one emergence hole x ¾. (After F. X. Williams).

of that very contact. This, again, has developed an immediate interest of the mother in her young comparable with what we observe in many birds. Probably this interest is aroused and sustained in the mother wasp by simple, pleasurable, chemical (odor) or tactile stimuli emanating from the egg and larva, but whatever be the nature of the stimuli involved, I believe that we shall have to admit that the egg and the larva have acquired a "meaning" for the mother wasp, and so far as the egg is concerned, this seems to be true even in the species that practice mass provisioning. We noticed that many solitary Vespoids (Eumenes, Odynerus), before they bring in their prey, carefully attach the egg by a string to the ceiling of the cell. This singular performance has been variously interpreted. Fabre and others regard it as a device for preventing the delicate egg from being crushed by the closely packed and sometimes reviving prey, on the same principle that in a crowded room an electric light bulb attached by a cord to the ceiling would be less easily crushed than one rigidly fixed to the walls or the floor. Others regard the filament as a device for keeping the egg free from the occasionally very damp walls of the cell. Ferton has recently shown that *Bembix mediterraneus* glues its slender egg to the floor of the cell in an erect position and with the base carefully supported by a cluster of large sand-grains (Fig. 28 A), and that *Stizus errans* glues its egg in a similar position to the top of a small, carefully selected pebble placed on the floor of the cell (Fig. 28 B). Parker's description of the egg of our *Microbembex monodonta* seems to indicate a condition similar to that of *B. mediterraneus.* In all these cases we seem to have an arrangement for keeping the very easily injured egg as free as possible from contact with the rough, sandy walls of the burrow. But even the Sphecoids and Psammocharids, which practice mass provisioning, attach the egg to a particular part of the victim and in such a position that the hatching larva can attack it at its most vulnerable point. Ferton, especially, has made a very interesting study of this type of behavior.

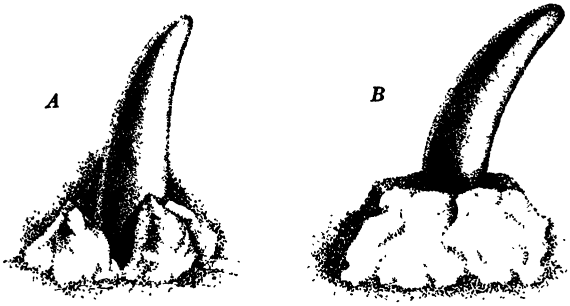

FIG. 28

A. Egg of *Bembix mediterraneus* with its base supported by a cluster of large sand-grains. *B.* Egg of *Stizus errans* glued to the upper surface of a carefully selected pebble. (After C. Ferton).

The following facts also indicate very clearly that the mother wasp may be aware, not only of sexual differences among her own eggs but also of the differences in the amount of food required by the resulting larvæ. Bordage, while investigating the Sphecoids of the Island of Réunion, found that three of the species, *Pison argentatum, Trypoxylon scutifrons* and *T. errans,* could be readily induced to make their cells in glass tubes placed between the

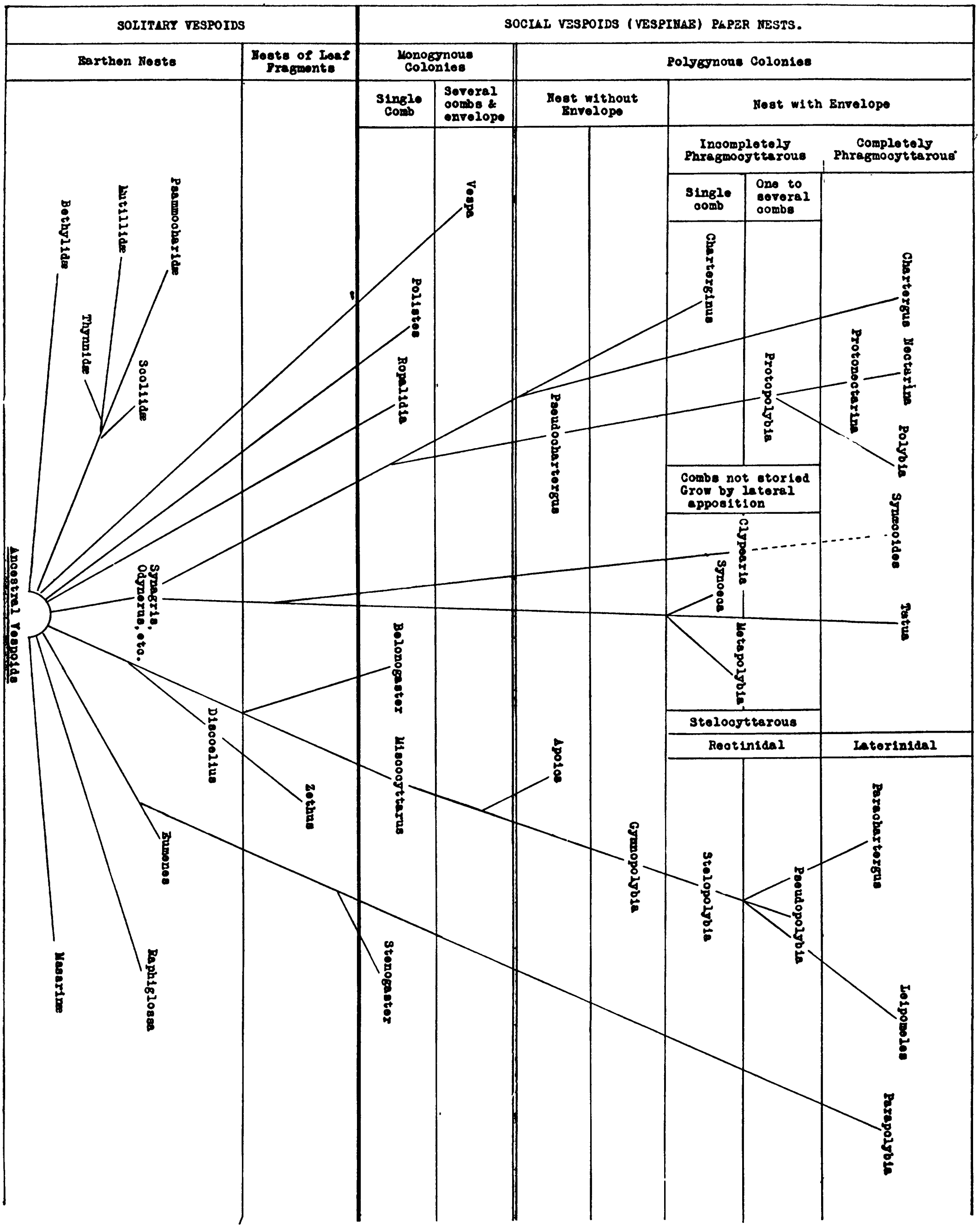

FIG. 29
Phylogenetic tree of the various genera and families of Vespoids. (After Ducke, with modifications).

pamphlets of his library. The Pison, under natural conditions, builds elliptical clay cells and provisions them with spiders, whereas the species of Trypoxylon nest in hollow twigs and the interstices of wall but use the same kind of prey. All these species adapted themselves to the glass tubes in the same manner. Each of them plugged the end of the tube with clay and divided the lumen into successive cells by building simple clay partitions across it. After the cells had been provisioned, Bordage observed that the first of them were longer by half a centimeter and contained more prey than those provisioned later, and he was able to show that the larvæ in the larger, more abundantly provisioned cells produced female, the others male wasps. Similar observations have also been published by Roubaud on the Congolese *Odynerus* (*Rhynchium*) *anceps,* which makes clusters of straight, tubular galleries in clay walls and divides each gallery into several cells by means of clay partitions. In this case also the first cells are much longer than the later, though there is no difference in the quantity of small caterpillars allotted to the different eggs. But Roubaud was able to prove experimentally that even when the amount of food is so greatly decreased that the larvæ produce adult wasps of only half the normal size, their sex is nevertheless in no wise affected. It would seem therefore that the mother wasp must discriminate between the deposition of a fertilized, female-producing and that of an unfertilized, male-producing egg, and regulate the size of the cell and in some instances also the amount of provisions accordingly.

In the accompanying diagram (Fig. 29), taken from Ducke but somewhat modified, I have indicated the hypothetical family tree of the solitary and social Vespoids. The genera below the heavy horizontal line are solitary, and among them Eumenes and Odynerus seem to be nearest to the original ancestors, because they are very similar to the social forms in having longitudinally folded wings and in other morphological characters. It will be seen that there are six independent lines of descent to the social forms above the heavy line and that the genera plotted at different levels represent various stages of specialization as indicated by the nature of the materials and types of structure of the nests. With the doubtful exception of a few Stenogastrinæ, all the social wasps make paper nests consisting wholly or in part of one or more combs of regular hexagonal cells, in which a number of young are reared simultaneously.

(*To be continued*)